

Adult population structure and behaviour of two seasonal generations of the European Map Butterfly, *Araschnia levana*, species with seasonal polyphenism (Nymphalidae)

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Summary. Adult population structure and behaviour of the spring and summer broods of *Araschnia levana* (Linnaeus, 1758) were studied in order to describe differences in ecological traits between seasonal generations of this polyphenic species. The more numerous summer generation had an unambiguously open population structure, while the population structure of the spring generation tended to be closed. Capture and estimated sex ratios were male-biased in both generations, probably owing to lower site tenacity of females. There were marked diurnal changes in behaviour of both generations. Both sexes fed on flowers during the mornings and late afternoons, while in the early afternoons males perched in aggregations with some features of typical leks. Females were only rarely seen during that time, their appearance provoked males to chase them. Butterflies of the summer generation spent more time nectaring, possibly owing to higher energy requirements associated with higher mobility. Males of the summer generation spent significantly more time flying or chasing as opposed to sitting on their perches, but this might have been a recording artefact. Seasonal alternation of dispersing and sedentary generations, combined with a lek assembly, might be the features which allow the species to respond rapidly to environmental changes.

Zusammenfassung. Struktur und Verhalten adulter Populationen von Frühjahrs- und Sommergenerationen von *Araschnia levana* (Linnaeus, 1758) wurden untersucht, um Unterschiede hinsichtlich ökologischer Parameter zwischen den saisonalen Generationen dieser polyphenetischen Art zu beschreiben. Die individuenreichere Sommergeneration zeigte eine eindeutige offene Populationsstruktur, während die Frühjahrsgeneration zur geschlossenen Populationsstruktur tendiert. Gesammelte und geschätzte Geschlechtsverhältnisse waren von Männchen dominiert, wahrscheinlich aufgrund geringerer Ortstreue der Weibchen. Es gab signifikante Unterschiede im Tagesrhythmus beider Generationen. Beide Generationen erscheinen in den Morgenstunden sowie am späten Nachmittag zum Nektarsaugen an Blüten, während sich die Männchen am frühen

Nachmittag in typischen Lek-artigen Aggregationen niederlassen. Weibchen wurden zu dieser Zeit nur selten beobachtet, ihre Erscheinung provozierte die Männchen sie zu jagen. Die Falter der Sommergeneration verbrachten mehr Zeit beim Nektarsaugen, möglicherweise um größere Energieressourcen anzulegen, die mit einer höheren Mobilität korrelieren. Männchen der Sommergeneration verbrachten signifikant mehr Zeit fliegend oder jagend anstatt sich niederzulassen, aber dies kann auch ein Beobachtungsartefakt sein. Saisonale Änderungen sich ausbreitender und seßhafter Generationen, kombiniert mit Lek-Ansammlungen, mögen die Voraussetzungen für diese Art sein, rasch auf Umweltänderungen zu reagieren.

Résumé. La structure et le comportement des populations d'adultes des générations printanières et estivales de *Araschnia levana* (Linnaeus, 1758) ont été étudiées afin de décrire les différences dans les affinités écologiques entre les générations saisonnières de cette espèce polyphénique. La génération estivale, qui est la plus abondante, a, sans ambiguïté, une structure ouverte alors que celle de printemps tend à rester fermée. La capture et la sex ratio des mâles est biaisée dans les deux générations, probablement en raison de la ténacité des femelles à occuper les sites bas. Il y a des changements diurnes marqués dans le comportement de chaque génération. Les deux sexes s'alimentent sur des fleurs le matin et tard dans l'après-midi, alors qu'en fin d'après-midi les mâles s'agrègent et se perchent avec quelques aspects comportementaux typiques. Les femelles sont rarement aperçues durant cette période, leur apparition conduisant les mâles à les chasser. Les papillons de la génération estivale passent plus de temps à s'alimenter, probablement en raison de leurs besoins de ressources en énergie plus intenses liés à leur plus forte mobilité. Les mâles de la génération d'été passent significativement plus de temps à voler ou patrouiller plutôt que sur leurs perchoirs, mais ceci pourrait être un artefact d'observation. L'altération saisonnière de dispersion et de sédentarité des générations, associée à un comportement de rassemblement, pourraient représenter des caractères permettant à l'espèce de répondre rapidement aux changements de l'environnement.

Key words: *Araschnia levana*, adult population, butterfly dispersal, lek, male assemblages, mate-locating behaviour, seasonal polyphenism.

Introduction

Seasonal polyphenism in butterflies is an adaptive trait, which allows species living in areas with changing but seasonally predictable climates, to avoid costs of genetic polymorphism while maintaining benefits of two adaptive strategies (Shapiro, 1976, 1980). The European Map Butterfly *Araschnia levana* (Linnaeus, 1758) (Nymphalidae) is a model example of seasonal polyphenism in butterflies. Adults of the spring generation (f. *levana*) are reddish with a fritillary-like black pattern, whereas the butterflies of the summer generation (f. *prorsa*) have white stripes on a black ground-colour and resemble black admirals (*Limenitis camilla*

(Linnaeus, 1764)) (Shreeve, 1992a). An occasional third (autumn) generation (referred to as f. *porima* or f. *intermedia*) is intermediate between the two. Proximately, the polyphenism is controlled by day length together with temperature and other cues which change regularly with time of year (Müller, 1955, 1956; Shapiro, 1976).

The species ranges throughout the Palaearctic, reaching Japan and the Russian Far East to the east (Korshunov, 1972; Korshunov & Gorbunov, 1995). The western edge of its distribution is situated in France, where the species is expanding westward and has reached the Atlantic coast but recently (Radigue, 1994–1995). In southern Europe, there are isolated populations in Spain (Higgins & Riley, 1980), the southern limits of the continuous European distribution of the species are found in northern Croatia and Romania (Niculescu, 1965) down to northern Greece (Koutroubas, 1991). The butterfly is relatively common in Central Europe. However, it is not as widely distributed as other nettle-feeding Nymphalids. The preferred habitats are wet meadows adjoining rivers and streams, river valleys and moist deciduous forests (Hrubý, 1956; Reinhardt & Richter, 1978, Ebert & Rennwald, 1991); it was reported that the species avoids early successional habitats (Steffan-Dewenter & Tschardtke, 1997).

Larvae of *A. levana* feed on nettles (*Urtica* spp.; in Central Europe only *Urtica dioica*). They live gregariously after emerging from the eggs, which are laid in a unique string-like pattern (Porter, 1992) on undersides of nettle leaves. The overwintering stage is the pupa.

Published studies of seasonal polyphenism in *A. levana* have so far focused on the developmental mechanism of the phenomenon and its relation to temperature change (Süffert, 1924), length of day (Müller, 1955, 1956; Reinhardt, 1969, 1984) or biochemical factors (Koch, 1996). On the other hand, field-oriented studies of the species' population ecology and behaviour are practically missing. The few published papers did not study the seasonal generations comparatively. Instead, they focused on habitat selection or climatic requirements of *A. levana* in comparison with closely related (in both taxonomic and ecological sense) species (Reinhardt & Richter, 1978; Reinhardt, 1984). The European Map Butterfly thus remains a surprisingly enigmatic species despite fairly good know-

ledge of proximate mechanisms of its polyphenism, extensive research conducted on other European nettle-feeding Nymphalids (Bryant *et al.*, 1997, and references therein) and at least two authors' (Brakefield & Shreeve, 1992) discussion of possible rewards of such studies.

We attempted to fill this gap in our knowledge and stated the following aims: (1) to compare adult population size and structure, mobility and other parameters of the two seasonal generations of *A. levana*, (2) to describe the behaviour of adults of *A. levana* in field conditions, to study their distribution, mating activities and changes of behaviour with time of day and (3) to look for differences, if any, between the spring and summer generations.

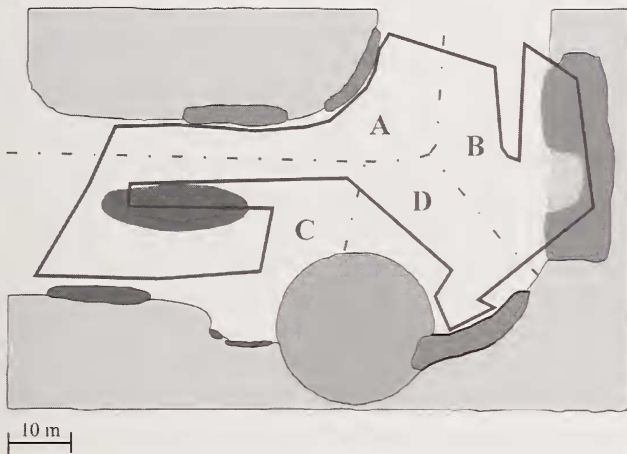


Fig. 1. Map of the study site showing the meadow (white), surrounding woody vegetation (light grey) and nettle patches (dark grey). The black line shows the position of the transect route; letters A, B, C, D are the subsites which were recognised for analysis. The grey circle is the large lime tree overseeing the meadow.

Methods

The lack of field research conducted so far on *A. levana* could possibly be explained by methodological problems inherent to working with common butterflies with open populations (see Shreeve, 1995). Given our previous experiences with *A. levana* and published information on closely related butterflies (tribus

Nymphalini) (Baker, 1972; Warren, 1992; Shreeve, 1995), we expected an open population structure. However, many of the methods used in this work are typically applied for butterflies which live in spatially restricted (closed) colonies (*sensu* Warren, 1992). When applying these methods, we understood this limitation but believed that our approach might at least indicate the most important trends, if not bring complete answers to the questions under study.

The fieldwork was carried out in the spring and summer of 1997, with additional observations in 1998. The study site (Fig. 1) was a moist meadow with dominant grass *Alopecurus pratensis*, 1.5 km south of Hluboká nad Vltavou, South Bohemia (49°02' N, 14°28' E, 375 m). The locality is situated within a varied landscape of meadows, fishponds, hedgerows and moist forests known as the České Budějovice Basin. The meadow was surrounded by habitats apparently unsuitable for *A. levana*: there was a mature oak-spruce forest on two sides, on one side there was a fishpond bank overgrown by reed, one side was delimited by a dense hedgerow along a water channel. Nettles (*Urtica dioica*) formed several distinct patches within the study site. We divided the meadow into four subsites which differed in the character of vegetation and distribution of nettles. Subsite A was a meadow-forest margin oriented to the South with nettles growing under the canopy; subsite B was a large nettle patch along a fishpond bank covered by reed; subsite C was in the centre of the meadow with nettles in sparse bunches interspersed with tall grasses; subsite D was a border between the meadow and a hedgerow with a large lime tree dominating the woody vegetation.

We applied three methods in the field. Population size and structure were estimated by (1) standard mark-release-recapture (MRR) techniques, (2) behaviour and diurnal activity were assessed by regular observations along a fixed transect and (3) by following of individual butterflies with portable tape-recorders.

For the MRR study, the butterflies were netted and marked by waterproof alcohol-based pens. We used the 1–2–4–7 system (Ehrlich & Davidson, 1960) with minute modifications. Wing wear (four categories as in Warren, 1987) was recorded for each captured butterfly.

Progressive estimates of butterfly numbers, obtained during one-day marking (Thomas, 1983), were calculated in order to detect whether the population of *A. levana* was closed or open. The results of such estimates should gradually improve in accuracy in a closed population, but increase meaninglessly if the population is open. The estimates for individual time intervals were obtained according to Craig (1953). The analysis was performed only on fine days, when the weather allowed continuous marking from dawn to dusk (May 17, 18 and 24, 1997 and May 9, 1998 for the spring generation and July 17, 28, 30 and August 5, 1997 for the summer generation).

Population sizes were estimated separately for generations and sexes. Numbers of individuals were calculated by the Jolly-Seber method, which allows for open populations (Jolly, 1965). Computing was done by program JOLLY, model A (Pollock *et al.*, 1990). Residence times were calculated using the formula $-\ln(\varphi)^{-1}$ (Cook, 1967; Tabashnik, 1980), mean residences per generation φ_A 's were obtained by the variance weighted averaging method (Tabashnik, 1980). Tabashnik's (1980) joint residence-catchability test and capture vs. estimated sex ratio test were performed in order to detect whether differences in numbers of males and females were caused by different residence or catchability of sexes. The joint residence-catchability test plots the natural logarithm of recapture probability ratio against time and allows a distinction between the effects of unequal residences and unequal recapture probability (between sexes). The capture vs. estimated sex ratio test estimates relative catchability of males and females for a sampling day and gives an average estimate for a set of dates (for details of the tests, see Tabashnik, 1980; Gall, 1984; Murphy *et al.*, 1986).

Behaviour was observed along a fixed transect route (about 400 m), which crossed the entire meadow (Fig. 1). We walked along the transect three times per hour and recorded the behaviour of all observed butterflies and the subsite where they were seen. We discriminated four subsites (see above) and seven types of behaviour: 1 – nectaring, 2 – flight, 3 – perching on herbaceous vegetation, 4 – perching on trees/shrubs, 5 – chasing with other butterflies, 6 – any behaviour unambiguously connected with reproduction (copulation, egg-laying etc.), 7 – resting. By definition, only males could

have been included in the "perching" categories. A butterfly was considered as "perching" when sitting on tops of herbaceous vegetation or at distal ends of tree/shrub branches; males sitting in lower layers of vegetation were listed as "resting". The data were analysed separately for generation, sex and part of day (morning vs. afternoon). Altogether, 70 transects were walked for the spring generation (May 15, 16 and 19, 1997) and 78 for the summer generation (July 17 and August 6 and 10, 1997).

Early in the course of the study, we noticed an aggregation of perching males regularly occurring at subsite B during the afternoon hours (see *Results* section). In both generations, we followed the males with a tape-recorder. We picked-up a sitting male and recorded its behaviour for the longest possible time, i.e., until the observer lost contact with the animal. The longest recorded observations lasted 837 and 641 seconds for males of spring and summer generations, respectively. The recorded observations were subsequently split into 2-minutes intervals for further analysis, and the observations shorter than 120 seconds were discarded. Flight, chasing, resting and basking were distinguished. The tape-recorded behavioural categories differed from those used for the transect analysis, because it was not possible to distinguish between "basking" and "perching" during the transect walks, while during the tape-recording we classified sitting with opened wings as "basking" and sitting with closed wings as "resting". (Also note, that the entire activity observed with tape recorders was perching.) For the spring generation, observations were carried out on May 17 and 23, 16 observations were analyzed and 49 discarded. The summer generation was observed on July 17 and August 3. Sixteen observations were analysed and 24 discarded.

All behavioural data were log-transformed to achieve normality and analysed using the *Statistica v. 5* (StatSoft Inc.) package.

Results

Population size and structure. The first individuals of the spring generation were observed on May 3 in 1997, the last specimen flew on May 28. The summer generation was on the wing from July 7 until August 28 in 1997. The progressive one-day estimates of population size (Fig. 2) indicated that the butterflies of the summer

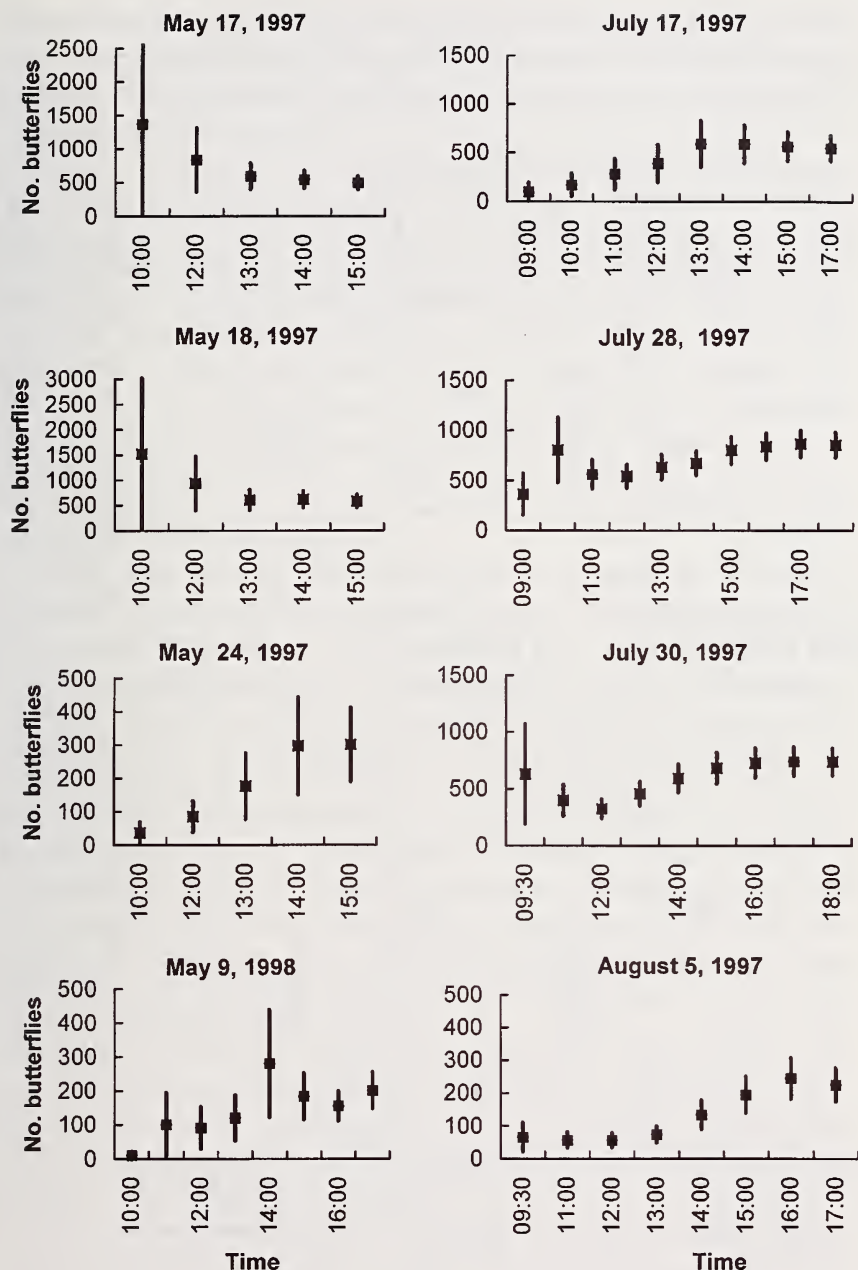


Fig. 2. Progressive one-day estimates of population size of the two seasonal generations of *A. levana*, with their respective standard errors. Left: spring generation, right: summer generation. Note that y-axes are not in scale.

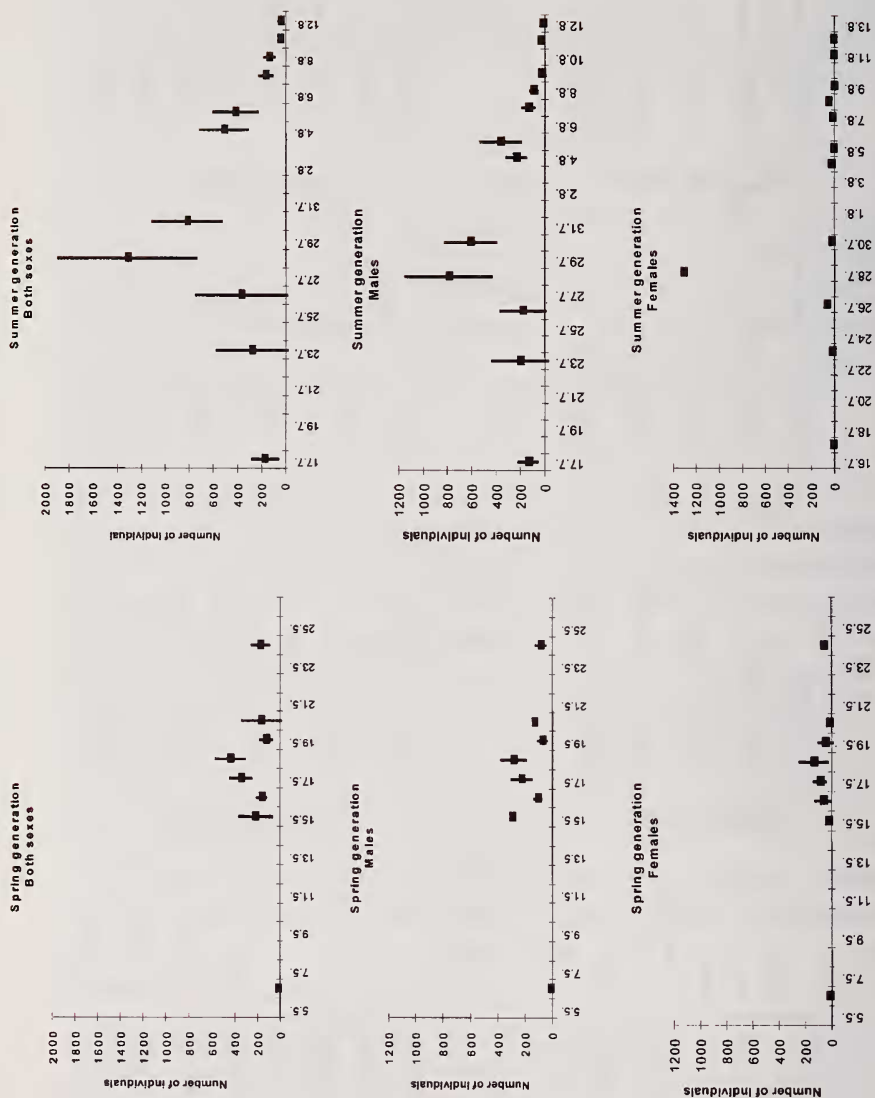


Fig. 3. Estimates of population size of spring and summer generations of *A. levana*, obtained by the Jolly-Seber method. Respective standard error bars are given only for those days for which they were computable from the data.

generation had a typical open population structure. The situation was more ambiguous for the spring generation, for which two repetitions of the experiment indicated a closed and two repetitions an open population structure.

Table 1 summarises daily catches of butterflies for MRR analysis. The Jolly-Seber estimates of daily numbers (Fig. 3) revealed that the adults of the summer generation were more abundant than those of the spring generation. Capture sex ratio males:females was male-biased in both generations (deviation from 1:1 ratio, spring: $\chi^2_{(1)} = 45.2$, $p < 0.001$; summer: $\chi^2_{(1)} = 1.64 \cdot 10^{-72}$, $p \ll 0.001$). The estimated sex ratios were also heavily male-biased (spring: $\chi^2_{(1)} = 9.7 \cdot 10^{-74}$, $p \ll 0.001$; summer: $\chi^2_{(1)} = 5.3 \cdot 10^{-78}$, $p \ll 0.001$). The prevalence of males did not change during their flight periods in both generations. However, the estimates for females, and the sex ratio estimates, were highly unrealistic due to low capture and recapture rates (see below).

There were no significant differences in single-day residences between males and females within the two generations (paired t-test, spring: $t_{(6)} = 1.13$, $p = 0.30$; summer: $t_{(7)} = -1.05$, $p = 0.33$). The residence statistics (Table 1) reveals shorter residence of males of summer generation. The joint residence-catchability tests were not significant for either generation. (Residence time males vs. females, spring: $F_{(1,4)} = 0.003$, $p = 0.96$; summer: $F_{(1,3)} = 0.96$, $p = 0.40$. Relative catchability males vs. females, spring: $t_{(4)} = 1.63$; $p = 0.18$; summer: $t_{(3)} = 2.41$; $p = 0.09$.) Therefore, the tests failed to distinguish whether the biased sex ratios were due to unequal residences or catchabilities. There were no significant differences with regard to residence and catchability between the generations (ANOVA comparison of the regression lines from the joint residence - catchability tests, residence: $F_{(1,7)} = 0.187$, $p = 0.68$; catchability: $F_{(1,8)} = 0.043$, $p = 0.84$). The capture vs. estimated sex ratio test did not reveal any significant difference in catchability among sexes of the spring generation ($\chi^2_{(1)} = 0.25$, $p = 0.62$), while males of the summer generation were significantly more catchable than females ($\chi^2_{(1)} = 106.04$, $p < 0.001$).

Wing wear was steadily increasing in spring males, spring females and summer males. In these cases, the increases were statistically significant (slopes of the regression lines of average wing

wears plotted against time, spring males: $F_{(1,8)} = 16.73$, $p < 0.05$; spring females: $F_{(1,8)} = 13.59$, $p < 0.01$; summer males: $F_{(1,12)} = 132.42$, $p < 0.01$). On the other hand, no significant trend was found for the wing wear progression of summer females ($F_{(1,12)} = 2.76$, $p = 0.12$).

Table 1. Summary of MRR catches and residence statistics of *Araschnia levana*. φ_i s are the estimated residences for individual periods, φ_A s are the mean residences per generation obtained by the variance weighted averaging method. Div/O denotes the periods for which the residence was not computable from the data.

	Males			Females		
	captured	recaptured	φ_i	captured	recaptured	φ_i
spring generation						
5 May	4	0		5	0	
6 May	9	1	0.25	10	1	0.20
15 May	62	0	0.93	26	2	0.84
16 May	38	14	0.62	9	1	0.50
17 May	42	10	0.90	21	4	0.91
18 May	73	26	1.13	28	9	1.22
19 May	24	17	0.34	7	2	0.21
20 May	5	0	0.33	2	1	0.37
24 May	42	11	0.92	8	1	Div/O
26 May	21	8		9	4	
mean residence (φ_A)			0.29			0.21
mean residence time (days)			1.8			1.5
Summer generation						
16 July	68	0		12	0	
17 July	74	16	0.47	15	1	0.09
23 July	48	4	0.77	18	0	Div/O
26 July	46	1	0.48	13	0	0.64
28 July	140	7	0.92	35	1	1.93
30 July	123	24	0.84	27	2	Div/O
4 August	51	12	0.76	27	0	Div/O
5 August	48	14	1.12	7	0	Div/O
7 August	42	11	0.48	7	0	0.58
8 August	40	16	0.56	9	1	1.22
9 August	25	16	0.26	9	3	0.11
11 August	23	6	0.61	11	1	0.33
12 August	20	7	0.26	7	2	0.55
13 August	11	3		4	2	
mean residence (φ_A)			0.43			0.50
mean residence time (days)			0.5			3.3

Behaviour, distribution. In both generations, there were marked differences in behaviour at different times of the day (see Figs 4, 5 for illustrative examples). Both sexes spent the morning hours nectaring on flowers, whereas most of the individuals disappeared from the observers' sight during noon (approximately from 12:00 AM till 1:00 PM) and were spotted only occasionally in the canopy of surrounding trees. Later, a distinct assemblage of males was daily observed on the sparse nettle bunches in the central part of the study site (subsite C). The males perched with closed wings on top of both nettle plants and grass blades (which were often topping the nettles). The average number of males which were seen perching in this site per transect was 5.3 in spring (40 "afternoon" transects, N = 223, SE = 2.14) and 6.4 in summer (44 transects, N = 275, SE = 3.98). Mutual chases among the males were frequent (spring: 86 chases tape-recorded; summer: 46 chases tape-recorded). The males often attacked other flying insects (one dragonfly, two bees, 14 peacocks — *Inachis io* (Linnaeus, 1758) — and 14 pierids). During this time, the females were practically absent from the meadow. If an occasional female showed up near the aggregation of males (four such observations were tape-recorded), her presence provoked repeated bouts of chasing, in which several males participated. The butterflies flew in ascending spirals during such chases, reaching about 10 m height above the meadow. Afterwards, the males either returned to the perching site or disappeared from sight.

Table 2. ANOVA results for behaviour of *A. levana* butterflies along the fixed transect.

Factor, interaction	d.f.	MS Effect	F	p-level
Generation	1,112	0,05	0,114	0,74; NS
Sex	1,112	16,10	40,613	<< 0,0001
Behaviour	6,112	18,41	46,446	<< 0,0001
Time of day	1,112	9,78	24,674	<< 0,0001
Generation-sex	1,112	0,18	0,448	0,51; NS
Generation-behaviour	6,112	4,03	10,162	<< 0,0001
Generation-time of day	6,112	7,82	19,725	<< 0,0001
Sex-behaviour	6,112	0,25	0,626	0,43; NS
Sex-time of day	6,112	9,26	23,377	<< 0,0001
Behaviour-time of day	6,112	6,64	16,758	<< 0,0001

In late afternoons, both sexes were again seen nectaring on flowers. On fine sunny days, the last individuals were nectaring until sunset.

Four-way analysis of variance of the behavioural observations from the transect (with the number of individuals as the frequency variable) (Table 2) confirmed the diurnal periodicity in behaviour and distribution of sexes. Sex, type of behaviour and time of day all had a significant effect on the number of individuals observed on the transect. Furthermore, the combined influences of factors generation-behaviour, sex-behaviour, time of day-behaviour and time of day-sex were also significant (Fig. 6). Butterflies of the summer generation spent more time feeding; only males were engaged in perching and chasing; perching and chasing were significantly more frequent during the afternoon hours.

Analysis of variance for distribution of butterflies within the study site (Table 3) revealed that both generation and sex significantly influenced butterfly distribution. Feeding subsites of the two generations differed according to distribution of nectar plants; males of both generations were more frequently encountered at subsite C, where they formed the afternoon perching aggregation (see above).

The analysis of tape-recorded behavioural observations revealed that the summer generation males spent less time flying/chasing and more time resting when compared with the spring generation (one-way ANOVA, $F_{(3, 82)} = 8.76$, $p < 0.001$).

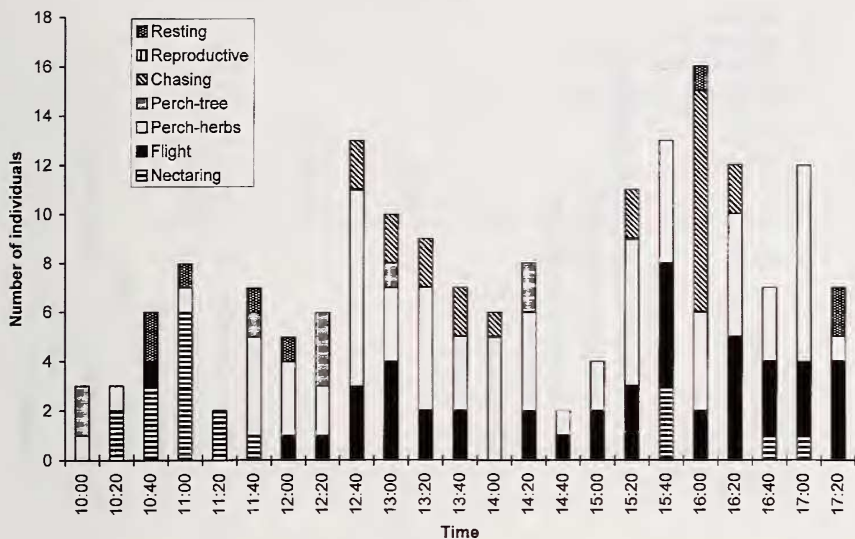
Table 3. ANOVA results for behaviour of *A. levana* butterflies along the fixed transect.

Factor, interaction	d.f.	MS Effect	F	p-level
Subsite	3, 56	7,98	7,976	< 0,001
Generation-subsite	3, 56	6,96	6,963	< 0,001
Sex-subsite	3, 56	3,19	3,199	< 0,05
Time of day - subsite	3, 56	1,15	1,148	0,34; NS

Discussion

Adults of the summer generation of *A. levana* were more abundant and less restricted in their movements. Both generations had

Spring generation - Males
May 16, 1997



Spring generation - Females
May 16, 1997

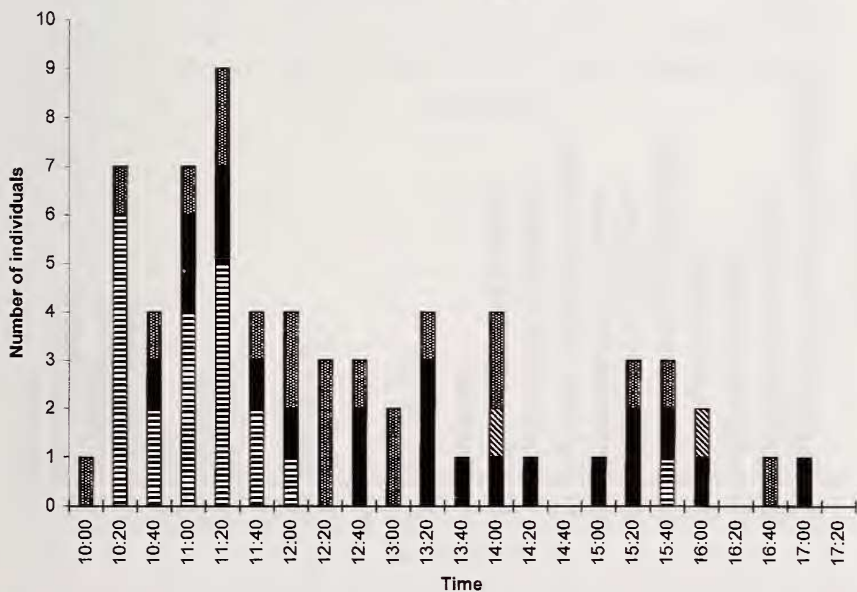


Fig. 4. Diurnal changes in activity of *A. levana*, adults of spring generation.

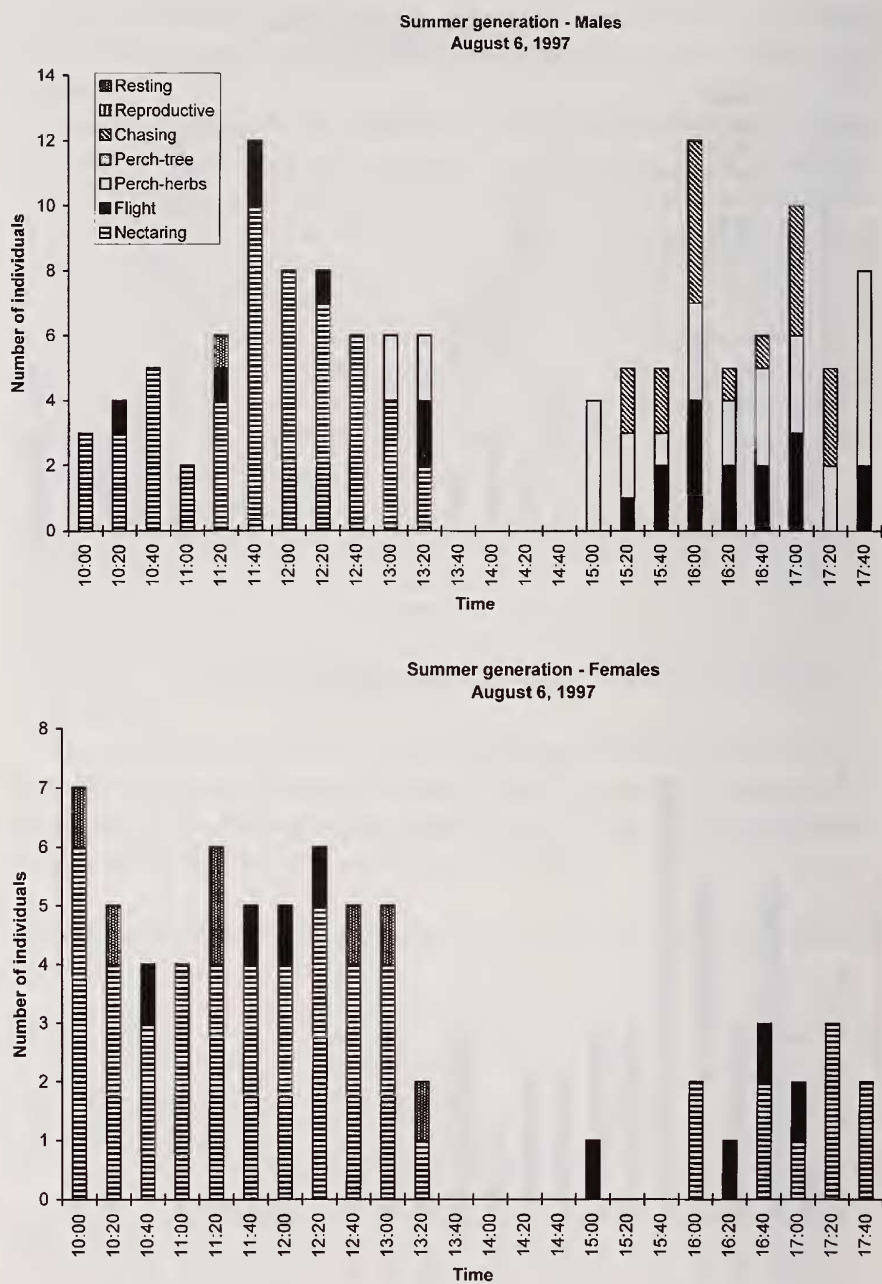
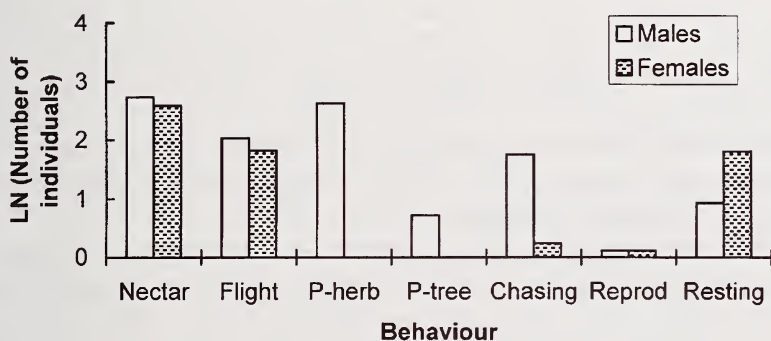


Fig. 5. Diurnal changes in activity of *A. levana*, adults of summer generation.

6a)



6b)



6c)

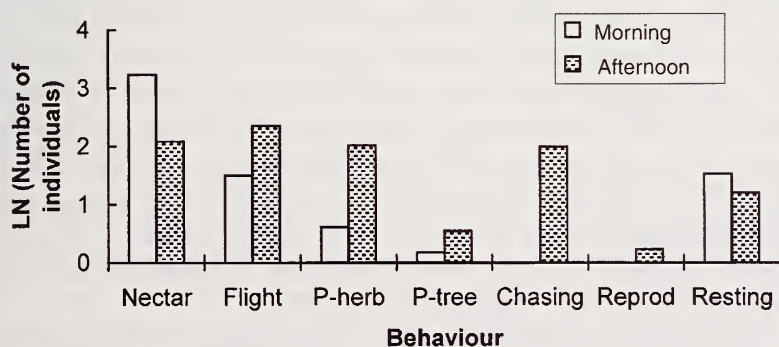


Fig. 6. Behaviour of *A. levana* adults as it was observed along the transect route (log-scale), with respective standard error bars: *a* – behaviour observed in spring vs. summer generations; *b* – behaviour observed for individual sexes; *c* – behaviour observed in morning vs. afternoon hours. Note the log-scale of y-axis.

male-biased capture and estimated sex ratios, their behaviour was characterised by predominance of nectaring in the morning hours and aggregate perching of males in the afternoon hours.

The lower abundance of adults of the spring generation suggests that the overwintering generation of *A. levana* might suffer high mortality during diapause. Host plants growing in spring usually have a high nutrient content (cf. Slansky, 1993) and, as a result, abundant progeny of the spring-flying adults replenishes the population numbers. This might correlate with different mobility of the two generations. Whereas the spring-flying adults might profit from not leaving the site where they successfully completed their development (such a site, by definition, provides all essential resources for them), it may be beneficial for individuals of the summer generation to leave. Higher population density of the summer generation may lead to competition for larval resources, this in turn lowering the emigration threshold (Baker, 1984). Differing mobility among generations has been assumed for several butterfly species and has been considered as one of the traits which allow multivoltine butterflies to become widespread in cultivated landscapes (Pollard & Eversham, 1995).

Three, admittedly circumstantial, lines of evidence suggest a higher mobility of the summer generation. First, the summer generation had a distinctly open population structure, while the situation was rather ambivalent in spring. Second, the females of the summer generation were rarely recaptured, being significantly less catchable than males. This trait caused the inflated estimates of their abundance (see Fig. 3). Third, the females of the summer generation did not show a significant increase of wing wear with time. This again suggests that they might not spend much time on the study site and instead might move rather freely across the landscape. Nevertheless, none of the arguments can be considered as a direct proof of higher mobility of the summer-flying adults, which might be obtained only by direct mark-release-recapture work covering a broader array of habitat patches (Hanski *et al.*, 1994; Sutcliffe *et al.*, 1997; Baguette *et al.*, 1998).

An intriguing problem, that recurrently emerges in butterfly population studies, is the male bias in both capture and estimated sex ratios (Scott, 1974, 1975; Daily *et al.*, 1991; Sutcliffe *et al.*, 1997).

Sexual differences in both distribution and behaviour are reported for many butterfly species (cf. Wiklund, 1977, 1982; Wiklund & Åhrberg, 1978; Baguette *et al.*, 1998). The sex-specific differences in both behaviour and distribution found in this study (Fig. 6, *b*) are the most plausible explanation of the biased sex ratios in *A. levana*. Males of both generations spent most of the days within the reach of observers, whereas the females regularly “disappeared” for several hours around noon. Furthermore, the males assembled at one site in the afternoon hours, which rendered them easily catchable. On the other hand, the joint residence-catchability tests failed to show significant differences between sexes in both residence and catchability. We assume that the failure was caused by the low number of females recaptured, in particular if more days elapsed between the first and subsequent captures. Consequently, the residence-catchability regression lines were constructed from too few points: compare the low number of degrees of freedom in our tests with those in Tabashnik (1980) and Gall (1984). It is notoriously difficult to separate different dispersal rates from different longevities (Tabashnik, 1980; Shreeve, 1992b, 1995); our residence statistics (see Table 1) do not suggest any conclusive solutions. Murphy *et al.* (1986) highlighted the necessity of nearly complete, labour intensive marking of the entire population, to obtain accuracy of such tests. This was admittedly not the case in this study, as the MRR days alternated with days devoted to behavioural observations.

Brakefield & Shreeve (1992) suggested the “fascinating” possibility that different wing colours of seasonal generations of *A. levana* might result into different mate-locating behaviours. They expected fritillary-like patrolling in the spring generation and admiral-like perching in the summer generation (vividly coloured butterflies tend to patrol rather than perch — Shreeve, 1992a). Our observation showed that in *A. levana*, males of both generations perch. Perching is restricted to the afternoon hours; in this respect, the diurnal changes in behaviour of *A. levana* resemble those of other European nettle-feeding Nymphalids (*Inachis io*, *Aglaia urticae* (Linnaeus, 1758) and *Vanessa cardui* (Linnaeus, 1758) — Baker, 1972; Scott, 1974). However, early morning perching was reported for some Nymphalids and the time of eclosion of females

was proposed as the explanation for the timing of activity of males (Rutowski *et al.*, 1996).

The perching activity in *A. levana* was characterised by the aggregation of males within one patch of the habitat, while the rest of the study site was virtually empty. Scott (1974) stated that perching should result to “distributing males more evenly throughout mating sites” due to mutual harassment in male to male encounters. In our study, nothing indicated any spacing apart — or territoriality — of males, which was described for other perching species (cf. Baker, 1972; Davies, 1978; Dennis & Williams, 1987; Rutowski *et al.*, 1996). In agreement with Knapton (1985), we suggest that such a situation might be interpreted as lekking, bearing in mind that the term may be used only in a relaxed sense for non-vertebrates (Lederhouse, 1982; Knapton, 1985; Alcock, 1987; Daily *et al.*, 1991; Shreeve, 1992a).

Typical lekking assemblages of males should, according to the original definition (Bradbury, 1977), occur at a place which lacks any larval or adult resources. Furthermore, individual males should monopolise exclusive patches within the lek and the males with the best (typically central) positions should enjoy most of the matings (Knapton, 1985; Wickman, 1985; Wickman & Jansson, 1997). The situation was different in *A. levana*, where the aggregation occurred at a foodplant patch. On the other hand, no other foodplant patch within the study site hosted such an aggregation and males competed for their perches as well as for females (e. g. the mutual pursuits). Also, we gained no evidence of females ovipositing (or hanging around) at the aggregation site, at least during the afternoon hours. Indeed, this would be disadvantageous for them due to continuous harassment by males. Further study should focus on elucidating the questions (1) where the ovipositions do actually occur and (2) whether the males compete for their positions within aggregation sites.

Although both the transect and tape-recorder results pointed to behavioural differences between generations, the evidence is weak and the interpretation of data is not straightforward. The behavioural differences between the generations documented in the analysis of the tape-recorder data may have been caused by the different colours of the seasonal morphs: the disruptive wing pattern

of the summer generation specimens might be responsible for the fast disappearance of flying/chasing males from the observers' sight. This alone would bias the data towards a higher proportion of the "resting" category. Moreover, a climatic (possibly temperature) element might have influenced the behavioural results and this question deserves a further, temperature-controlled study. On the other hand, the transect-gained observation that butterflies of the summer generation spent more time nectaring seems to be robust. This might be explained by higher energy requirements of the more active summer generation of these ectothermic insects.

Pollard & Eversham (1995) speculated that widespread British butterflies, such as nettle-feeding Nymphalids, benefited from changes brought by modern agriculture (e.g. fertilizers) and became more abundant recently than they had been in the past. Recently, *A. levana* has indisputably become a common species in Central Europe. Although our evidence is only circumstantial, it is possible that the habit of alternating sedentary and dispersing generations, when the sedentary generation stays in more favourable habitats and the dispersing generation leaves these in search for new space, combined with a lek-assembly mating system (which ensures that the sexes meet despite their dispersing habits), might allow the species to respond rapidly to changing natural conditions and to fluctuate in range and abundance. Such fluctuations are indeed documented in literature (Hrubý, 1956; van Swaay, 1990; Beneš & Kuras, 1997) and there is evidence of recent range expansion and occasional migrations along the southern, western and northern edge of the range (Koutroubas, 1991; Radigue, 1994–1995; Bradley, 1998).

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